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TEMPORAL COMPARISONS OF REEF FISH POPULATIONS AT MIDWAY ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

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INTRODUCTION

In spring 1992 the Protected Species Investigation (PSI) of the Southwest Fisheries Science Center, Honolulu Laboratory, began evaluation of a recent decline in the Hawaiian monk seal, Monachus schauinslandi, population at French Frigate Shoals (FFS), a multi-atoll islet located 750 km northwest of the main Hawaiian Islands in the Northwestern Hawaiian Islands (NWHI). Initial results indicated that the primary cause of the decline in seal condition and densities at FFS was related to a deficient forage base, particularly for younger seals.

To investigate the hypothesis that the observed changes might be linked to reduced prey abundance, the PSI then enlisted the help of personnel from the Insular Resources Investigation (IRI), who conducted a study to determine whether a decline had occurred at FFS in fish stocks that are potential prey for seals. Personnel of the Hawaii Cooperative Fishery Research Unit (HCFRU), formerly of the U.S. Fish and Wildlife Service (USFWS), had estimated fish densities at a series of shallow reef stations at FFS in the early 1980s, at a time when the FFS seal population was larger but healthier. In July 1992, fish stocks at these same stations were reassessed using identical diver-observation methods by IRI personnel. Results suggested (DeMartini et al., 1993) that fish densities averaged about one-third lower in 1992, compared to 1980-83, at stations near commonly used haul-out areas in the northern region of the FFS atoll (Craig et al., To date, the food limitation hypothesis remains a 1992). reasonable possibility, and quantification of the forage base of monk seals in the NWHI is a continuing interest. This is particularly true for sites where monk seals are presently underpopulated, and where translocations of seals to rebuild populations are planned. Midway Atoll, about 700 nmi northwest of FFS in the NWHI, is one such site. The purpose of this study was to investigate whether stocks of shallow reef fishes at Midway had detectably declined between 1980 and 1993.

METHODS

Sampling Stations and Surveys

During 1980, personnel of the HCFRU, USFWS (now National Biological Survey, NBS), conducted a series of surveys of the densities of shallow-water demersal fishes at Midway Atoll in the NWHI. These surveys complemented those of predator-prey relationships (Parrish et al., 1985; Norris and Parrish, 1988) and related (e.g., Schroeder, 1985, 1987, 1989) studies of the reef communities at Midway and at FFS. At that time, HCFRU personnel surveyed stations in barrier reef (BR; inside, outside) and patch reef (PR) habitats at Midway; a variable number of stations were sampled on two surveys conducted during March-April

and August-September 1980. In August 1980 they surveyed nine stations; both primary types of shallow-reef habitats were sampled with approximately equal effort. Four stations were located in expansive BR habitats, and five PR stations were sited in the lagoon of the atoll (Fig. 1). A total of 18 transect counts were made at the nine stations (Appendix Table 1).

Eight of these nine historical (hereafter referred to as "test") stations were relocated on the August 1993 survey. During August 7-13, reef fish densities were estimated at these eight test stations, and at two additional "nontest" stations sampled during March-April 1980 (BR station number 4 and PR station number 5) plus another (PR station number 9) whose location was approximate. In addition, for each test and nontest station, a second ("reference") station, 100 to 300 m distant, was newly sampled in August 1993 to provide context for interpretation of larger spatial patterns. Altogether, a total 44 transects (11 pairs of stations by 2 samples station of larger completed on the August 1993 survey. Fish densities were estimated using techniques identical to those used in August 1980.

Habitat Descriptions

Barrier reef habitats included stations both inside and outside the atoll. "Outside" stations were typical "spur-and-groove" habitat (>90% dead coral rock, <10% interdigitating sand channels), exposed to open ocean swell. Outside stations had sparse live coral cover (<1% Pocillopora meandrina), and were sited at 5- to 8-m depths in expansive (continuous, from 0- to >20-m depths) habitat. "Inside" barrier stations consisted primarily of micro-atolls of Montipora spp. corals (one-third to three-fourths live coral cover), plus coral rubble and sand, and were sited in similarly expansive (but more wave-protected) areas within the lip of the barrier reef at <1- to 3-m depths.

Lagoonal patch reefs consisted of low- (<1-m) to moderate- (2- to 3-m) relief mounds of consolidated dead coral rock and unconsolidated coral rubble at 4- to 10-m depths. Live coral cover on patch reefs was generally low (<5% Porites spp.) but varied among reefs, as did the types and amounts of algal cover.

Sampling Methods

Methods can be summarized as follows (for further details see DeMartini et al., 1993): Divers visually enumerated all non-cryptic (mostly day-active) fishes present on belt transects (Brock 1954) or within otherwise delimited areas of reef during daylight (0800-1700) hours. A two-diver team always conducted simultaneous fish counts at a station.

Belt transects of constant dimensions (50 m long by 10 m wide; $500-m^2$ area) were surveyed in expansive BR habitats, and at

one large patch reef (PR nontest station number 16) sampled in 1980 only. A 50-m-long line divided the transect area into two contiguous and parallel strips (each 50 m long by 5 m wide). Starting at the same end of the transect, the two-person team (Divers 1 and 2) first swam out along the length of the transect. Divers 1 and 2 proceeded abreast (5 m apart) and each tallied fish encountered within each of five, end-on-end, 10-m-long by 5-m-wide (50-m²) quadrats, on left (L) and right (R) sides of the line, respectively. The divers then switched sides, reversed direction, and swam back along the length of the transect, so that Diver 2 surveyed the strip just surveyed by Diver 1, and vice versa. In this manner, each diver tallied fishes within the same series of 10, 10 m long by 5 m wide quadrats, and each diver's total count represented a single density estimate (number of fish per 500 m²). Approximately 30 minutes was spent surveying the transect strip by each diver. Fishes were tallied as encountered, by species (or lowest recognizable taxon).

At most PR stations, divers were able to census entire habitats by cordoning reefs into 4 to 8 (2 to 4 L plus 2 to 4 R), approximately 5 m long by 5 m wide, quadrats within approximately 100-200 m² search areas that included the reef's fringing sandrock ecotone. Divers 1 and 2 each enumerated all the fishes encountered in a quadrat-by-quadrat search, following the procedure used for transects at the BR stations. Each diver's total count thus represented a single density estimate (number of fish per 100-200 m²). These fish-count censuses required about 30 minutes. As for belt transects at BR stations, one pair of censuses was conducted at a PR station on a given date. Tape measurements of average reef diameter were used to estimate the area of each reef-station, assuming a spherical shape (reefs were roughly elliptical to circular in outline). Appendix Table 1 provides the estimated areas of each station (listed by sampling period because areas of emergent substrate vary seasonally and annually in the sandy-bottomed Midway lagoon: Schroeder, 1989).

Quadrat-specific data were not included in our analyses (see below). Specific sampling protocols, however, importantly influence transect estimates (Sale and Sharp, 1983), and it would be essential to repeat our protocols exactly if surveys are to be quantitatively duplicated in the future. Detailed protocols are therefore provided herein for future reference.

Body size distributions of fishes were characterized using in situ visual length estimates on the August 1993 survey. (Body length data were not collected on the August 1980 survey.) While two divers were estimating or censusing the numbers of fishes, the third diver estimated the lengths of all fishes encountered on a haphazard, 30-minute swim throughout the general station area (while avoiding the other two divers). Post-recruit-stage (>1-cm standard length, SL) fish encountered within a 1- to 3-m distance of the diver were tallied by length class. Length-

classes were progressively broader for larger fish, as follows: 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm, 5-6 cm, 6-7 cm, 7-10 cm, 10-15 cm, 15-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, >50 cm.

The three members of the dive team were rotated between the density and length estimation tasks to randomize diver effects among stations. This precaution minimizes the effects of potential differences among divers at the expense of some loss in precision (DeMartini et al., 1989).

Data Analyses

Our analyses were directed toward answering the following major questions: (1) Were historical test stations representative of larger spatial patterns in reef fish abundance at Midway in August 1993? (2) Had fish assemblage composition and relative abundance changed between the 1980 and 1993 August surveys? (3) Had the densities of any common and abundant species, feeding guilds, trophic levels, or total fishes changed between 1980 and 1993?

Analyses focused on potential temporal patterns for total reef fishes in both habitat types. In addition, we explored whether temporal changes were detectable for either of the two major trophic levels (primary consumers or "herbivores," secondary consumers or "carnivores") that comprise total fishes. We further evaluated each of four foraging guilds included within the carnivore level: benthic invertebrate-feeders, hereafter referred to as "benthic carnivores"; "zooplanktivores"; "corallivores"; and "piscivores." Recorded taxa were classified into trophic levels and foraging guilds using Hobson (1974), Randall (1985), and Norris and Parrish (1988). Omnivores were assigned entirely to one or the other trophic level based on whether animal or plant matter dominated the diet; analogous decisions were made for carnivore guilds. Counts of taxa were summed within levels and guilds prior to analyses. Sampling efforts focused on estimating densities of higher taxonomic categories, in part because of the likely poor statistical resolution of species-level data, and in part because the specific prey of monk seals is not well known (DeMartini et al., 1993).

As a prelude to our primary comparisons of fish densities between sampling periods (described below), 2-way ANOVAs were used to test for effects of major reef type (BR, PR) and station type (test, reference) on fish density for stations sampled on the August 1993 survey. These preliminary ANOVAs evaluated the following categories: total fishes, herbivores, total carnivores, each of the four carnivore guilds, and each of 15 species that were common and abundant in both BR and PR habitats during August 1993. "Inside" and "Outside" BR habitats were analyzed as one entity because data were too few to warrant partitioning into two microhabitats.

For all ANOVAs and primary temporal comparisons of densities (t-tests, see below), data were log-transformed to improve the normality of distributions, and a "1" was added to avoid the undefined logarithm of zero (necessary for all specific taxa and carnivore prey guilds). In order to minimize the effects of "adding 1" for taxa with zero densities, data were first standardized to N·ha (where 1 ha = $10^4 \ \text{m}^2$).

Fish assemblage structure was evaluated in terms of the relative commonness and relative abundance of species.
"Commonness" was evaluated as frequency of occurrence (i.e., the number of transects at which a species occurred) and "abundance" by estimated density on transects. Spearman's rank correlation and Kendall's coefficient of concordance (Siegel and Castellan, 1988) were used to test for similarity of assemblages between habitat types and sampling periods. Evaluations focused on the top 20 taxa within rankings, in order to avoid inherent bias towards concordance (similarity among rankings) when rare, invariably low-ranked, taxa are included in comparisons (Kobayashi, in prep.).

Matched-pairs designs were used for primary analysis of temporal patterns in density, with the data matched by sampling station and paired by the time period ("Before": August 1980; "After": August 1993) in which samples were collected. Both parametric (paired t-test) and nonparametric (matched-pairs signed-ranks test) procedures were used. The basic datum analyzed was the (rank) density for each sampling location and time period; a constant two, repeat counts were averaged and this mean used to represent the basic datum. For paired t-tests, the test variable was the "delta" (before minus after period difference) of the station-specific estimate. The nonparametric analogue of this variable was the signed-rank of the station-period difference (Siegel and Castellan, 1988). Thus, sample size and statistical power were determined by the number of test stations sampled (BR: 4; PR: 4; total: 8), rather than the total number of samples or transects.

Simple t-tests also were calculated for density data unmatched by station and the results compared with those of the paired t-tests, as a check on the effect that pairing by station had on the temporal comparisons. $Log_{10}~(x+1)$ station means (as above) were used as test variables; and Satterthwaite's approximation (Bailey, 1981) was used to reduce degrees of freedom appropriately if variances remained heterogeneous following transformation. Standard errors of the station means also were used to estimate spatial variation in abundance among stations within each of the two sampling periods. Estimated means were back-calculated from geometric means.

Statistical analyses used the procedures PROC MEANS, RANK, CORR, TTEST, and GLM of the Statistical Analysis System (SAS,

1987). Siegel and Castellan (1988) was consulted for binomial tests. Two-tailed probabilities (α_2) were used except when a one-tailed test (α_1) of a specific prediction was more appropriate. Type I error was relaxed to 0.10 in order to increase statistical power (1 minus Type II error; Cohen, 1988), as suggested necessary by analogous data for reef fishes at FFS (DeMartini et al., 1993). Bonferroni's inequality (Harris, 1985, p. 7) was used to adjust probability values for n multiple comparisons (alpha_{crit} < alpha_{0.10}/n) as necessary.

Statistical power was evaluated for matched-pair t-tests, using log-based means and deltas, based on observed changes in major taxa and taxonomic groupings of fishes. The sample sizes required for detecting changes of defined magnitude also were estimated. Sample size estimates assumed approximately normal distributions of the deltas; sample size estimates further assumed that an equal number of samples would be collected in each of two sampling periods.

Length frequency counts (August 1993 data) were converted to biomass using the weights of mid-point length classes estimated from specific length-weight regression parameters (J.D. Parrish, unpubl. data). Estimated weights were summed over all taxa for total fishes and summed separately for component herbivores and carnivores.

RESULTS

Test vs. Reference Station Comparisons

For stations sampled on the August 1993 survey, the densities of most higher-level taxa, and some specific taxa, clearly differed between reef types (PR>BR; Tables 1 and 2; also see "Assemblage Structure" below). The densities of almost all higher-level taxa, however, were equivalent at test and reference stations (Table 1). Test and reference stations also were indistinguishable for most key individual taxa (Table 2). These observations indicate that subsequent analyses, including primary comparisons between sampling periods, should be stratified by reef type a priori, and that data should be pooled over reef types only if habitats are indistinguishable for particular cases. We therefore follow with an evaluation of assemblage structure that acknowledges likely habitat differences within our temporal comparisons of primary interest.

Assemblage Structure

Tables 3 and 4 characterize the commonness and abundance of major fishes at Midway Atoll during the two sampling periods. Table 3 lists the top 30 (top 20 plus 10 additional, for context) most frequently encountered fishes on the August 1980 survey (ranked by the number of full transects on which they occurred);

the relative frequency occurrence of these same fishes in August 1993 is also noted. Table 4 similarly lists the top 30 most numerous fishes in August 1980 (ranked by density), with the analogous rankings for August 1993 noted. The 30 rankings listed in Tables 3 and 4 are based on pooled occurrences and grand mean densities, respectively, using all within-period data for both reef types. Table 5 further specifies density rankings of the top 30 taxa within each major reef type. For completeness, all taxa encountered on the two August surveys at Midway are listed in Appendix Table 2.

For the top 20 most numerous fish taxa at Midway, ranks of densities were significantly concordant between the two sampling periods for data pooled over the two major habitats (Kendall's Coefficient of Concordance with k=4, W=+0.442, P<0.001). Ranks of frequencies and ranks of densities, pooled over habitat types, were correlated between sampling periods (frequency: Spearman's rho = +0.77, P<0.01, Table 3; density: rho = +0.63, P<0.01, Table 4). Ranks of densities within habitat type were also correlated between sampling periods (BR: rho = +0.80, P<0.01, PR: rho = +0.637, P<0.01, Table 5). Rankings diverged more between the two habitat types, both in August 1980 (rho = <0.01, P>>0.05) and in August 1993 (rho = +0.14, P>0.05; Table 5).

Survey presence-absence. -- Of the taxa observed in August 1980, those most conspicuously missing in August 1993 included two corallivores (the butterflyfish Chaetodon multicinctus and the blenny Exallias brevis), and two herbivorous surgeonfishes (Acanthurus olivaceus, and the clown kala Naso lituratus).

Several other, clearly recognizable species that were observed in 1993 were not recorded on the 1980 survey. These included one nocturnal benthic carnivore (the lionfish, Pterois sphex); and a number of diurnal benthic carnivores, particularly the goatfish Parupeneus bifasciatus and two labrids (the cigar wrasse, Cheilio inermis; and juveniles and adults of the rockmover wrasse, Novaculichthys taeniourus).

Altogether, nine taxa of conspicuous, easily recognizable reef fishes were seen on the August 1980 survey but were not observed in August 1993, compared to eleven taxa recorded in 1993 but not seen in 1980 (accept $H_o\colon P\to A=A\to P;\ P>0.41;\ Table 6)$. About 90% of the conspicuous taxa, among the 90-100 total taxa observed on the two August surveys, were observed on both surveys (Appendix Table 2).

Other specific taxa of nontrivial abundance during either 1980 or 1993--that contributed strongly to overall patterns of change between the two surveys--are treated in greater detail in the section below on "Temporal Density Comparisons."

Habitat effects.—Notwithstanding these general temporal consistencies, there were many conspicuous and persistent differences at species (and higher) levels between the barrier and patch reef fish faunas. Among the most notable of these were several diurnal invertebrate feeders that were consistently more common and abundant on patch reefs, including the labrids Coris venusta and Labroides phthirophagus and the butterflyfish Chaetodon fremblii. Two carnivorous cirrhitids occupied distinctly different coral habitats—the arceye hawkfish (Paracirrhites arcatus) was sighted only in Pocillopora meandrina coral heads at outer barrier reef stations, whereas most Paracirrhites forsteri were seen occupying live and dead finger corals (Porites compressa) on patch reefs. A nocturnal benthic carnivore (the scorpaenid Dendrochirus barberi) occurred only on patch reefs. One relatively large-bodied, non-corallivorous butterflyfish (Chaetodon auriga) was always common only at inside barrier reef stations. Most piscivores (except the large, freeranging carangids) were consistently more common and abundant on patch reefs; key representatives were both diurnal (lizardfishes, family Synodontidae) and nocturnal (moray eels, Gymnothorax spp, family Muraenidae).

Among diurnal zooplanktivores, the damselfish Chromis ovalis was consistently better represented at patch reef stations. Another planktivorous damselfish (Dascyllus albisella) and the planktivorous butterflyfish Chaetodon miliaris were much more abundant on patch reefs during both surveys. Apogonids, a common and abundant taxon of nocturnal zooplanktivores, were always abundant on patch reefs only.

Herbivores, especially Kyphosus spp. (K. bigibbus), subadult and adult parrotfish (Scarus perspicillatus), and several surgeonfishes (primarily Acanthurus nigroris, A. leucopareius, and A. triostegus) were consistently better represented at inside or outside barrier reef, compared to patch reef, stations. A conspicuous exception was the herbivorous damselfish Stegastes fasciolatus, always more abundant on patch reefs.

These specific examples of survey and habitat differences further illustrate that similarities generally dominated differences in the Midway reef fish assemblage temporally (between sampling periods), but that assemblages more frequently differed spatially (between barrier and patch reef habitats).

Temporal Density Comparisons

Estimates of the numbers of fish individuals per standard ($10~\text{m}^2$) area are listed for each of the top 30 taxa on August 1980 baseline transects (all stations pooled; Table 5). Table 5 also lists the densities of each taxon in August 1993 and its habitat-specific density during each sampling period. These top

30 taxa accounted for 87-96% of the total fishes present on transects, depending on habitat and period (Table 5).

Most of the apparent, before-after changes in densities of specific taxa were decreases (Table 5). Taxa with the greatest declines between 1980 and 1993 (with relative density for the two surveys noted in parentheses) included one nocturnal benthic carnivore, the patch-reef squirrelfish Neoniphon [Flammeo] sammara (8x); and several diurnal planktivores--Dascyllus albisella (2x) on patch reefs, Chromis ovalis in both habitats (4x), the barrier reef damselfish C. hanui (25x), and the patch-reef butterflyfish Chaetodon miliaris (2x).

Counter to the major trend of lower numbers in 1993, a small number of striking recent increases were apparent (Table 5). The foremost of these were two patch-reef species, the goatfish Parupeneus pleurostigma (20x) and the labrid Cheilinus bimaculatus (30x), as well as two labrids that occurred in both habitats but increased most dramatically on patch reefs, Coris venusta (4x), and Anampses cuvier (6x).

Matched-pair t-test comparisons were unable to detect significant ($\alpha_{\rm crit} = \alpha_{2,0.10}/36 = 0.0028$) temporal changes, however, for any of the 36 taxa that ranked within the top 30 in frequency or abundance at one or both major habitats (Table 7).

The general inability to detect large changes was due to great variability: standard deviations of the differences (\log_{10} - based) averaged 1.07 (range 0.14 - 2.03) among the 36 taxa tested. Standard deviations of the deltas used in the paired-difference tests were equivalent (nominally 11% larger) than the average of the standard deviations (0.96) of the unmatched station means used in simple t-tests. Nominal changes at test stations ranged from a 97% decrease ($Chromis\ hanui$; P = 0.022 ns) to a 43x increase ($Parupeneus\ pleurostigma$; P = 0.058 ns). In general, species-level data provided virtually no resolution (see discussion on "Power of Temporal Comparisons").

A suggestion of pattern emerges if the sign (direction) of nominal change is evaluated for the same 36 test taxa: decreases outnumbered increases (25 versus 11; P = 0.015; binomial test; Table 7).

A stronger temporal pattern emerges when carnivore taxa are evaluated as functional categories; density changes were detectable for most carnivore guilds. By matched-pair t-test, an apparent decrease of 21% in benthic carnivores approached significance at P = 0.04 (Table 8). Evidence for a decrease of seemingly greater magnitude (60%) in planktivores, however, was weak (P = 0.15; Table 8, Fig. 2). An even larger (79%) decrease in piscivore density was highly significant (P = 0.002; Table 8;

Fig. 2). Among carnivores, only corallivores clearly showed no evidence of temporal change (Table 8).

A pattern of temporal change becomes even more apparent when higher functional categories such as trophic levels are examined. Herbivores ("primary consumers") and carnivores ("secondary consumers") exhibited 27-32% declines (Fig. 2) that approached statistical significance (Table 8). Overall, the density of total fishes declined by about one-third at both BR and PR test stations (Table 8, Fig. 2). Herbivores contributed about one-third and carnivores about two-thirds to total fish counts in both habitats during the August surveys in both 1980 and 1993 (Fig. 2).

For the various pooled taxa, the standard deviations of the log-based differences used in matched-pair t-tests averaged 0.41. As with specific taxa, this average was equivalent to (nominally 8% lower than) the average of the standard deviations of the unmatched station means used in simple t-tests.

Nonparametric (matched-pair signed-ranks) tests produced results qualitatively similar to matched-pair t-tests for the same pooled taxa (Table 9). These results suggest that the parametric paired t-tests were not compromised by the normality assumption.

Spatially, the observed declines were extensive for both trophic levels and component carnivore guilds (Table 10). Herbivores declined an estimated 37% on the barrier reef and 15% on patch reefs. Declines in carnivores were an estimated 21% at barrier-reef and 41% at patch-reef stations. Before-after declines in carnivore guilds (excluding the extremely variable corallivore data) deviated only 10-16% between the two habitat types (Table 10).

In summary, the overall decreases in fish density we observed at Midway between the August 1980 and 1993 surveys included herbivores as well as carnivores, occurred in both major reef habitats, and comprised nominal decreases for numerous specific taxa (Tables 7-10).

August 1993 Size Composition and Biomass

Figure 3 illustrates the size composition of fishes at the two primary reef habitats in August 1993; data are presented separately for herbivores (primary consumers) and carnivores (secondary consumers) in panels A and B, respectively. Relatively greater numbers of large (16-40 cm SL) herbivorous fishes occurred at barrier, compared to patch reef, stations, even though more moderately small (7-11 cm SL class) fish were tallied on the barrier reef (Fig. 3A). The length distribution of carnivores (Fig. 3B) also was skewed towards larger-bodied

fishes on the barrier reef (mode at 11-15 cm SL) compared to the patch reefs (7-11 cm SL).

The length composition of carnivores is further partitioned into trophic guilds in Figure 3B. In both BR and PR habitats, zooplanktivores dominated the smaller size classes (\leq 7-11 cm SL), and benthic carnivores were better represented at larger body sizes (Fig. 3B). Corallivores and piscivores, both relatively minor components, were represented at body sizes below and above the 7-11 cm SL mode, respectively (Fig. 3B).

In August 1993, fish biomass densities on Midway's shallow coral reefs averaged about $0.8-1.8~\rm kg\cdot 10~m^{-2}$ (at 12 fish·10 m⁻² weighing a mean 70-150 g each). For both habitat types pooled, herbivores contributed a little less than one-half, and carnivores slightly more than one-half, to total fish biomass (Fig. 4).

Total biomass density was about 40% greater on patch reefs (1.4 kg·10 m⁻²) than on the barrier reef (1.0 kg·10 m⁻²). Contribution by trophic level differed between barrier and patch reef habitats; herbivores and carnivores each represented about one-half of total fish biomass on the barrier reef, whereas carnivores clearly dominated fish biomass on patch reefs (75%; Fig. 4).

DISCUSSION

Representativeness of Test Stations

Densities of higher-level taxa and key individual taxa were indistinguishable between historical test stations and reference stations, the latter newly established on the August 1993 survey, despite sufficient power to detect average two- to threefold differences between reef types for seven higher taxa. It should not be surprising that fish densities were alike at test and reference patch reefs, since the areas of these two types of patch reef stations were the same (test: mean = 116 m^2 , CV = 43%; reference: mean = 112 m^2 , CV = 57%; Appendix Table 1). (Also see section on "Reef Area vs. Fish Density," below.) These observations indicate that our test stations are generally representative of the major habitats at Midway Atoll. We further conclude that the pooled (test plus reference) station data provide the most comprehensive and accurate description of the fish fauna at Midway during August 1993 and justify our use of all station data to characterize the faunas present in each August survey.

Reef Area vs. Fish Density

It is possible that our temporal comparisons of fish densities on patch reefs would have been compromised if the sizes

of the reefs differed systematically between the 1980 and 1993 surveys so that densities estimated in 1993 either over- or underrepresented actual abundances. This could result from the strong inverse relation between reef size and fish density on Midway patch reefs (Schroeder, 1989), reflecting ecotone (perimeter-to-area) effects described elsewhere by others (DeMartini et al., 1989; Ambrose and Swarbrick, 1989). Fluctuations in patch reef sizes (Schroeder, 1989) in fact might cause fish densities to differ more greatly over time at one reef, than at different reefs estimated concurrently. densities would have been underestimated in 1993 if, for example, reef areas were then generally larger than in 1980 because the 1993 survey occurred by chance at a time of lesser sand burial. That both surveys were conducted in August makes seasonal effects unlikely. However, interannual differences in sand inundation have been observed for patch reefs in Welles Harbor (Schroeder, 1989). A simple comparison of the areas of the four test PR stations, measured in 1980 and again in 1993 (Appendix Table 1), though, suggests no pattern (matched-pair t-test; B-A delta-bar = $+37 \, \text{cm}^2$, t = 0.9, P>0.5, 3 df; PRs No. 6, 11, 17, 18). This observation gives us further reason to believe that the declines in fish densities we observed in 1993 are real.

Assemblage Structure

The basic structure of the fish assemblages on shallow Midway reefs was similar in August 1980 and August 1993. The similar-sized species lists of the two surveys (90-100 non-cryptic taxa) likely reflects a balance between the more than twofold (22/9) greater number of 1993 stations (area) searched and the somewhat finer taxonomic resolution with which fishes were recorded on the 1980 survey. Species density might have been depressed along with numerical densities (DeMartini et al., 1993) on the 1993 survey. The greater areas of reef surveyed in 1993 likely offset the taxonomic detail in 1980, thus the similar number of P→As and A→Ps noted in Table 6.

The observed greater similarity over time within habitat type, compared to persistent differences in both the composition and relative densities of certain species between habitats, mirrors our observations at FFS in July 1992 (DeMartini et al., 1993). Randall et al.'s (1993) qualitative description of a persistent, but typically habitat-specific, assemblage of fishes at Midway further supports our conclusions. In general, there are few differences between our 1993 observations and those of Randall et al. (1993) in 1989/1991-92, with regard to the characteristic habitats of the common and abundant fishes at Midway.

Temporal persistence in the assemblage structure and habitat specificity of fishes has been observed in studies of other coral reef systems (e.g., DeMartini et al., 1993), with some

interesting exceptions (Sale et al., 1984; reviewed by Sale, 1980, 1991). In light of our observations (this study), the more interesting question is not whether assemblage structure differs (according to some statistical criterion) between August samplings in 1980 and 1993, but, rather, what real changes in reef fish abundances, specifically or generally, might represent. Do changes in abundance of some (but perhaps not other) taxa merely represent chance differences in recruitment success and subsequent year-class establishment among species, as noted previously for Hawaiian reef fishes (Walsh, 1984, 1987)—consistent with the so-called "lottery" model (Sale, 1980, 1990, 1991)? Might changes in general abundance levels also reflect large-scale ecosystem processes (Doherty and Williams, 1988; Doherty, 1991), perhaps even involving some deterministic component (Roberts, 1991)?

The general nature of the observed declines at Midway (involving both herbivores and carnivores) suggest that ecosystem-level effects, transcending the stochastic recruitment of particular (groups of) species, are involved at least to some extent. Most taxa of reef fishes are zooplanktivorous during pelagic larval stages, regardless of whether they are carnivorous or herbivorous after settlement onto reefs (Leis 1991). If food resources ever limit the population numbers of reef fishes, decreases in water-column productivity during pelagic larval stages should have greater general influence than decreases in one of the many component forage bases (Parrish et al., 1985; Norris and Parrish 1988; Parrish 1989) of resident-stage reef fishes. The implications of this argument will be developed further in the section below on how long-term variations in oceanic productivity might have affected the abundance levels of NWHI reef fishes.

Temporal Declines in Fish Stocks

The broadscale (herbivore plus carnivore) declines in fish densities at Midway contrast with the declines in carnivores versus distributional shifts in herbivores observed at FFS in July 1992 (DeMartini et al., 1993). The observed lack of change in overall herbivore densities at FFS in 1992 seemed to reflect a net increase at patch reefs canceling a net decrease at barrier reef stations (DeMartini et al., 1993). Density estimates for herbivores at FFS in 1992 were confounded by strong shifts in the spatial distributions of many (primarily surgeonfish) taxa between barrier and patch reef habitats. Lower densities of carnivorous fishes (including some major component feeding guilds) at FFS in 1992 were not confounded by distributional shifts and probably represented decreases in abundance throughout both barrier and patch reef habitats. The decreases in herbivorous fishes we observed at Midway in 1993 quite likely reflect responses to decreased levels of productivity, as observed for carnivorous fishes at FFS in 1992 (DeMartini et al., 1993).

A key issue is why reef fish declines crossed trophic levels at Midway, but were confounded by distributional shifts in herbivores only at FFS. The data for herbivorous fishes and algae at FFS suggest one possible explanation. Herbivores (primarily surgeonfishes) had increased disproportionately on patch reefs at FFS in 1992, compared to 1980-83, along with the percentage cover of one algal taxon (Microdictyon spp.) that is an important food resource for grazers of filamentous algae (Jones, 1968). DeMartini et al. (1993) speculated that the Microdictyon bloom at FFS in 1992 resulted from recent storm destruction of live coral habitat and a subsequent proliferation (See Delasalle et al., 1993 for another example of of algae. increased primary production on and near coral reefs induced by storm disturbance.) Perhaps the effects of storm disturbance and increased nutrient availability during 1977-88 (see below) were weak or absent at Midway by 1993. Interestingly, corallivore densities at Midway were clearly unchanged between 1980 and 1993. This contrasts with the marked declines in corallivores at FFS between 1980-83 and 1992 (DeMartini et al., 1993). For whatever reasons, Microdictyon was generally rare on patch reefs (and the barrier reef) at Midway in 1993 (authors' observ.), as during 1980 and 1981-85 (Schroeder, 1989; R. Schroeder, pers. commun.). The persistent low abundance of herbivores (relative to carnivores) on patch reefs at Midway would be expected if the abundances of algae on patch reefs were similarly low during both August surveys.

The general decreases in reef fishes we observed at Midway may have been influenced by interdecadal changes in ecosystem productivity in the central Pacific, north of the Hawaiian Islands (Polovina, 1994; Polovina et al., 1994), as previously suggested by DeMartini et al. (1993) for FFS. During the period from about 1977 to 1988, many major storm events generated unusually turbulent conditions that increased nutrient availability within the photic zone of near-Hawaii waters and might have stimulated primary productivity. This increase might have led to higher productivities of lobster, seabirds, and monk seals at FFS during the eighties. The "declines" observed at Midway and at FFS after 1988 may be viewed as returns to more "normal", lower levels of productivity (Polovina, 1994; Polovina et al., 1994). The recent apparent declines in reef fishes thus may reflect a more typical level of fish abundance, when the carrying capacity of fishes (and their predators) on shallow reefs in the NWHI is lower. Some of the changes in reef fish numbers at Midway and FFS may represent lagged numerical responses to fluctuations in recruitment resulting from altered levels of planktonic productivity. Such responses in population numbers as a whole are buffered by age structure against the fluctuations of individual year classes (DeMartini et al., 1993).

The observed declines in Midway reef fish stocks can be reexpressed in terms of decreased production, given several assumptions. The assumptions are that declines in numbers

approximate declines in standing biomass (see "Summer 1993 Biomass," below), and that an overall mean mortality rate (M = Z) for unexploited Midway reef fishes is equal to the ratio P:B (Allen, 1971), where P = production and B = biomass. If Z remains constant, equals 1.5 on average for tropical reef fishes (Ingles and Pauly, 1984), and standing biomass declined by about $0.3-.4~\rm kg\cdot 10~m^{-2}$, then the rate of production (as P = Z·B) of Midway reef fishes was $0.45-.6~\rm kg\cdot 10~m^{-2}$ less in August 1980 than in August 1993. If true, the production of reef fish prey in fact declined to a biologically meaningful extent.

Other Comparison Data

Few quantitative data exist on within- or among-year variations in fish population abundances at Midway or elsewhere on shallow NWHI reefs. Randall et al.'s (1993) overview of the Midway fish fauna, although an invaluable contribution, is largely qualitative. And the data of Hobson (1980, 1984) and Okamoto and Kanenaka (1984) for Midway and other NWHI reefs are semiquantitative or undocumentable, respectively.

With the exception of DeMartini et al.'s (1993) analysis of 1980-83 versus 1992 data for FFS, only Schroeder's (1989) data provide a quantitative measure which can help interpret the temporal patterns of numerical change we observed for Midway fishes. During a 51-month period from May 1981 to August 1985, Schroeder (1989) censused the abundances of recruit and resident fishes on numerous patch reefs, including many of the same HCFRU stations, in Welles Harbor at Midway. At quarter-year intervals, a total of 19-21 censuses were conducted at each of four control (unmanipulated) patch reefs ranging in size from 10 to 150 m². Total counts (recruits plus residents of all species pooled)
generally fluctuated less than one-third within reefs, except during brief but large summertime recruitment spikes. Variation in total counts among the five August surveys (1981-85, inclusive) was somewhat greater (CV = 45%; Schroeder, 1989, Fig. 5.8); however, three species (the fantail filefish *Pervagor* spilosoma, Dascyllus albisella, and Apogon maculiferus) together comprised nearly one-half of the 1981-85 totals (ibid, p. 175 and Table 4.3). During the August surveys of 1980 and 1993, filefish were rare, and the pooled densities of *Dascyllus albisella* and apogonids differed little if at all (15%; Table 5, this study). The magnitude of the declines in total fishes that we observed in between 1980 and 1993 August surveys thus slightly exceeds the average magnitude of seasonal variation, and clearly exceeds the variation among Schroeder's (1989) five August surveys, during the presumed period of higher productivity and abundance. While not conclusive in itself, this information tends to support our conclusion that the lower abundances in 1993 are real.

Power of Temporal Comparisons

To date, most evaluations of spatial differences and temporal changes in reef fishes have been nonparametric comparisons of rank abundance (e.g., Jones and Thompson, 1978), multivariate characterizations of composition (Bortone et al., 1986), or have focused on comparisons of sampling methods (references in Bortone and Kimmel, 1991). Presumably because of large natural variability, few studies (e.g., Thresher and Gunn, 1986; Green and Shenker, 1993) have attempted to evaluate statistical power to detect spatial differences or temporal changes in reef fish densities, particularly at the species level. The "before" versus "after" data of this report thus provide one of the few data sets available which can be used to estimate statistical power in tests of whether reef fish populations have changed over time.

The statistical power of the Midway data is either encouraging or discouraging, depending on the taxonomic resolution desired. Clearly, sampling efforts similar to those conducted are inadequate for detecting less than huge (>>100%) changes in species abundance. Impractically large sample sizes would be required to detect declines of reasonably large (say twofold; Skalski and McKenzie, 1982) magnitude for most individual species. For example, detecting twofold changes for 7 of the top 10 most common and abundant species listed on Table 5 would require from 25 to several hundred samples (where each sample is a station, sampled before and after with two repeat counts), depending on species. Only three species (the Pacific gregory damselfish, Stegastes fasciolatus; the belted wrasse, Stethojulis balteata; and the saddleback wrasse, Thalassoma duperrey—the latter being Hawaii's most common and abundant shallow—reef fish (Hourigan and Reese, 1987)—would likely (at power ≥ 0.80) require about a dozen or fewer samples (<8 to 15 at $\alpha_2 = 0.05$; <8 to 12 at $\alpha_2 = 0.10$).

Power to detect twofold changes in higher-order taxa, however, is acceptable (≥ 0.80) at practical sample sizes (< 8-12 samples) for total fishes, for each major trophic level and for most carnivore guilds (Table 11). If the question asked is answerable at higher taxonomic levels or other larger groupings (as in the case of the fish prey of monk seals), then using visual diver surveys to estimate reef fish densities is a reasonable undertaking. On the other hand, if species-level discrimination is required, much greater sampling effort would be required.

Matched-pair sampling and analysis designs, in which stations provide their own spatial controls, can appreciably improve statistical power to detect temporal changes. The 1980-83 versus 1992 comparisons of reef fishes at FFS (DeMartini et al., 1993) provide one clear example. Our 1980-93 comparisons

for higher taxa of reef fishes at Midway (this study) provide relatively weak support for the advantage of matched-pair designs, perhaps because the large temporal declines that we observed overwhelmed the spatial differences among stations. No benefit was found in unmatched designs, though, and we continue to recommend that matched-pair designs be used whenever possible.

Summer 1993 Biomass

Total counts of fishes at Midway in August 1993 were about one-third lower than during August 1980 (Fig. 2). Based on these fish count data (and assuming body size distributions were similar during August 1980 and August 1993), the standing biomass of fishes at Midway was equivalently low in August 1993 (Fig. 4). August 1993 estimates of the mean standing biomass of fishes on shallow Midway reefs are nonetheless almost twice as high as present average values for fishes on shallow reefs in the MHI (0.4-0.6 kg·10 m⁻²; R. Brock, Hawaii Inst. Mar. Biol., pers. comm., Sept. 1992; 0.65 kg·10 m⁻²; Grigg 1994). DeMartini et al. (1993) noted a similar difference between FFS and the MHI.

Although diver counts are more likely to under- than to overestimate fish abundances (Sale and Douglas, 1981; Davis and Anderson, 1989), the consistently narrow transect widths used throughout our study probably minimized the degree of underestimation (Sale and Sharp, 1983). We consider it unlikely that the apparent difference between Midway and the MHI is an artifact of different sampling methods because MHI researchers use similarly short and narrow transects. Rather, the difference might reflect the present heavily exploited condition of fish populations on shallow reefs in the MHI (Grigg, 1994).

We believe that our August 1993 biomass density data are reasonable estimates of absolute values that can be used for subsequent quantitative comparisons of the diurnal, non-cryptic fishes on shallow Hawaiian reefs. In the future, any real differences between the MHI and the NWHI could contribute important information to be used in the development of management plans for shallow-reef resources in the MHI.

SUMMARY AND CONCLUSIONS

The abundances of fishes on shallow (<10-fm) coral reefs at Midway Atoll, Northwestern Hawaiian Islands, were sampled by trained divers using identical visual-survey techniques during two August surveys 13 years apart. A baseline or "before" period survey (defined after the fact) was conducted in August 1980. An "after" survey was completed in August 1993. Numerical density estimates were compared between the two periods using a "matched-pair" design where samples were matched by station.

Eight of nine possible stations were sampled with equal effort (two repeat counts) during each August survey. Equal effort was distributed across two primary shallow-reef habitat types. Four stations were located in expansive habitat on seaward and leeward barrier reefs; four stations were isolated patch reefs within the lagoon of the atoll. Stations were located offshore and to the northwest, west, and southwest of beaches on the west side of Sand Island, a region frequently used by monk seals as a haul-out area.

Our analyses produced the following major results:

- Fish assemblages differed little between the two sampling periods in terms of the relative commonness and abundance of individual species. Similarities overshadowed differences in assemblage structure temporally. There were, however, notably persistent differences in assemblage composition and relative abundance between barrier and patch reef habitats.
- Matched-pair comparisons indicated significant changes for none of three dozen test taxa, but species-level differences were difficult to evaluate because of low statistical power.
- A suggestion of pattern emerges if the sign of nominal changes in densities is evaluated; apparent decreases significantly outnumbered increases at the species level.
- Patterns of temporal change become more apparent when higher level taxonomic categories are used. Patterns of decline were similar for major trophic levels (herbivores and carnivores) and for most component feeding guilds within the general carnivore or secondary consumer level, as well as for total fishes.
- Available data provide sufficient statistical power to meaningfully evaluate major groups (trophic levels, feeding guilds) of fish taxa.
- The results of our temporal comparison of fish densities at Midway (as at FFS; DeMartini et al., 1993) are consistent with but do not prove that the abundance of the shallow-reef fish prey of monk seals has declined to a biologically meaningful extent (standing biomass: 0.3-.4 kg·10 m⁻²; production: 0.45-.6 kg·10 m⁻²) between 1980 and 1992-93 at NWHI reefs. Also (as we have cautioned previously: DeMartini et al., 1993), it is unknown to what extent the day-active fishes on shallow reefs contribute to the diet of seals, especially juveniles. Obviously, our observations have less relevance if night-active fishes (e.g., apogonids, holocentrids), octopus, or lobster dominate the diet of juvenile seals.

August 1993 size-composition data allowed us to estimate the current biomass densities of fishes on shallow Midway reefs. Biomass estimates for Midway reef fishes in 1993 were similar to those estimated for FFS in July 1992 and seem about twice as high as typical values for shallow coral reefs in the MHI. This difference may reflect the present highly exploited state of reef fish populations in the MHI, relative to reef fish populations on pristine reefs of the NWHI. This speculation requires further study.

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TABLES



Table 1.--Summary results of 2-way ANOVAs evaluating the effects of reef type (REEFTYP, barrier = BR versus patch reef = PR) and station type (STATYP, test versus reference, see Methods) on density (N·10 m⁻²) of reef fishes observed at Midway Atoll, Northwestern Hawaiian Islands, on the August 1993 survey. Taxa were classified by major trophic level and by feeding guild within the carnivore level. Degrees of freedom for all F-ratio tests were 1,41 (i.e., Error df = 41, based on 44 total transects, partitioned as 20 BR + 24 PR, and as 22 test + 22 reference). REEFTYP x STATYP interaction terms were insignificant in all cases (P = 0.25-0.75). Alpha-levels were adjusted for multiple comparisons using the Bonferroni inequality (see text).

		REEFT		STATYP				
	F-	Duch	N •	10 m ⁻²	-	D }-	N•10	m ⁻²
	ratio	Prob >F	BR	PR	F- ratio	Prob >F	Test	Ref
Total fishes	45.05	<.001ª	8.0	17.3	0.14	.71	12.0	12.5
Herbivores	9.52	<.01 ^b	3.5	5.3	0.03	.87	4.4	4.4
Secondary consumers	51.17	<.001 ^b	4.3	11.6	0.15	.70	7.2	7.6
Benthic carnivores	6.78	.013°	3.5	5.4	0.32	.57	4.7	4.3
Planktivores	47.47	<.001°	0.1	4.1	0.33	.57	0.7	0.9
Corallivores	7.93	<.01°	.08	.02	3.16	.08	.06	.02
Piscivores	11.77	.001°	.02	.09	6.51	.015°	.02	.08

^{*}Significant at $\alpha_{2,\text{crit}} \leq .10$

bSignificant at $\alpha_{2,crit} \leq .10/2 \leq .05$

[°]Significant at $\alpha_{2, \text{crit}} \leq .10/4 \leq .025$

Table 2.—Summary results of 2-way ANOVAs evaluating the effects of reef type (REEFTYP, barrier = BR versus patch reef = PR) and station type (STATYP, test versus reference) on density (N·10 m⁻²) of 15 taxa of reef fishes observed as common and abundant (see text) in both BR and PR habitats at Midway Atoll, Northwestern Hawaiian Islands, on the August 1993 survey. Degrees of freedom for all F-ratio tests of main effects were 1,41. See table 1 caption for explanation and for additional ANOVA test details. Significant REEFTYP x STATYP interactions are flagged for 4 taxa excluded from further analysis. Significance of main effects is also based on the Bonferroni inequality.

		REEFTYP					STATYP				
	F-	Desch	N·10	m ⁻²	_	•••	N·10	m ⁻²			
Taxon	ratio	Prob >F	BR	PR	F- ratio	Prob >F	Test	Ref			
Anampses cuvier	[F-rati	o = 8.0	8, P =	.005ª 1	for (RE	EFTYP :	x STATY	P)]			
Bodianus bilunulatus	[F-rati	o = 12.	45, P =	.001ª	for (R	REEFTYP	x STAT	'YP)]			
Coris venusta	10.06	.003ª	.019	.170	6.03	.018	.028	.147			
Labroides phthirophagus	3.50	.068	.0079	.038	0.00	.985	.0190	.0187			
Stethojulis balteata	0.04	.84	.164	.184	0.04	.83	.165	.185			
Thalassoma ballieui	6.56	.014	.344	.052	0.68	.41	.166	.091			
Thalassoma duperrey	3.44	.071	.707	1.953	0.11	.74	1.027	1.276			
Chaetodon miliaris	140.9	<.001ª	10-4	.263	0.00	.98	.022	.021			
Abudefduf abdominalis	[F-rat	io = 16	.03, P<	.001ª f	for (RE	EFTYP :	x STATY	P)]			
Chromis hanui	0.39	0.54	.0022	.0012	0.04	0.83	.0018	.0015			
Chromis ovalis	0.13	0.72	.0100	.0146	0.41	0.53	.0171	.0088			

Table 2.--Continued.

		REEFT	ΥP			STAT	ΥP	
	-	5 1	N·10 m ⁻²				N·10 m ⁻²	
Taxon	F- ratio	Prob >F	BR	PR	F- ratio	Prob - >F	Test	Ref
Stegastes fasciolatus	0.10	0.76	2.003	2.167	0.51	0.48	2.284	1.913
Scarid juveniles	24.55	<.001ª	.008	.360	6.64	0.014	.025	.175
Acanthurus triostegus	[F-ra	atio = 8	8.06, P	= .007	a for (REEFTY	P x STA	ATYP)]
Ctenochaetus strigosus	3.56	0.07	.0264	.0055	0.20	0.66	.0138	.0096

 H_o : BR = PR H_a : BR ≠ PR

 H_o : Test = Reference H_a : Test \neq Reference

8/11 PR>BR; P>0.32

7/11 Test>Reference; P = 0.24

^{*}Significant at $\alpha_{2,crit} \leq .10/15 \leq .0067$

Table 3.--Estimated absolute and relative (rank) frequency occurrence (on transects) for the top 30 fish taxa encountered at Midway Atoll, Northwestern Hawaiian Islands, on the August 1980 baseline survey (18 transects). Also listed are the absolute frequencies and rankings of these 30 taxa on the August 1993 survey (44 transects). A dashed horizontal line separates the top 30 baseline taxa in August 1980 from lower-ranked taxa that ranked within the top 30 on the 1993 survey.

Frequency occurrence (No. transects) and rank frequency occurrence

Taxon	August	1980	August	1993
Stegastes fasciolatus	18	3	44	1
Thalassoma duperrey	18	3	42	2
Stethojulis balteata	18	3	41	3
Thalassoma ballieui	18	3	35	5.5
Scarus perspicillatus	18	3	23	13.5
Chaetodon fremblii	16	6	31	7.5
Labroides phthirophagus	15	7	26	9.5
Paracirrhites forsteri	14	9	22	16.5
Chromis hanui	14	9	10	34.5
Ctenochaetus strigosus	14	9	23	13.5
Synodontid spp.	13	13.5	15	28.5
Coris venusta	13	13.5	35	5.5
Canthigaster jactator	13	13.5	20	20
Chaetodon miliaris	13	13.5	23	13.5
Plectroglyphidodon johnstonianu	s 13	13.5	19	22
Kyphosus spp.	13	13.5	21	18.5
Parupeneus multifasciatus	12	18	3	63.5
Bodianus bilunulatus	12	18	26	9.5
Chromis ovalis	12	18	19	22
Cheilinus unifasciatus	11	22	4	53.5
Gomphosus varius	11	22	9	37
Cirrhitops fasciatus	11	22	17	24
Dascyllus albisella	11	22	16	26
Macropharyngodon geoffroy	11	22	22	16.5
Abudefduf abdominalis	10	26	24	11
Scarid juveniles	10	26	31	7.5
Acanthurus triostegus	10	26	23	13.5
Apogon spp.	9	28	11	32.5
Parupeneus pleurostigma	8	30.5	21	18.5
Anampses cuvier	8	30.5	40	4
Coris flavovittata	8	30.5	16	26
Cirripectes spp.	8	30.5	9	37
Acanthurus nigroris	7	36	19	22
Thalassoma purpureuma	5	48.5	16	26
Chaetodon auriga	7	36	15	28.5
Parupeneus porphyreus	6	43	14	30

^{*}Recorded as Thalassoma fuscum on August 1993 survey.

Table 4.--Estimated absolute and relative (rank) abundance (numerical density, N·10 m⁻²) for the top 30 fish taxa encountered at Midway Atoll, Northwestern Hawaiian Islands, on the August 1980 baseline survey (18 transects at 9 stations). Also listed are the absolute densities and rankings of these 30 taxa on the August 1993 survey (44 transects at 22 stations). A dashed horizontal line separates the top 30 baseline taxa in August 1980 from lower-ranked taxa that ranked within the top 30 on the 1993 survey.

, and the second	umerical De	ensity	(N·10 m ⁻²)	& Ranks
Taxon	August	1980	August	1993
Stegastes fasciolatus	3.02	1	2.78	1
Dascyllus albisella	2.51	2	1.05	4
Thalassoma duperrey	2.44	3	2.17	2
Chromis ovalis	1.41	4	.34	11
Stethojulis balteata	.68	5	.41	8
Chromis hanui	.57	6	.02	46
Chaetodon miliaris	.55	7	.30	12
Apogon spp.	.45	8	1.53	3
Acanthurus triostegus	.45	9	.18	16
Cirripectes spp.	.44	10	> .02	40
Thalassoma ballieui	.42	11	.43	7
Ctenochaetus strigosus	.42	12	> .12	21
Labroides phthirophagus	.36	13	< .15	19
Scarid juveniles	.29	14	1.02	5
Kyphosus spp.	.28	15	.20	14
Calotomus spp.	.28	16	.19	15
Aulostomus chinensis	.17	17	.02	45
Paracirrhites forsteri	.17	18	.08	23
Bodianus bilunulatus	.17	19	< .12	22
Abudefduf abdominalis	.15	20	< .39	10
Scarus perspicillatus	.14	21	> .06	28
Chaetodon fremblii	.14	22	.15	18
Dendrochirus barberi	.14	23	.02	42
Cirrhitops fasciatus	.12	24	.03	35
Scorpaena spp.a	.12	25	< .01	64
Neoniphon sammara	.11	26	.02	43
Coris venusta	.11	27	.39	9
Acanthurus nigroris	.10	28	> .12	20
Gomphosus varius	.10	29	< .02	51
Acanthurus olivaceus	.10	30	.00	ь
Parupeneus pleurostigma	< .03	 59	.47	 6
Anampses cuvier	.04	50	.24	13
Cheilinus bimaculatus	< .01	88	.16	17
Plectroglyphidodon johnstoni		38	< .08	24
Synodontid spp.	.09	35	.07	25
Canthigaster jactator	.09	33	.07	26
•				

Table 4.--Continued.

	Numerical Density	(N·10 m ⁻²) & Ranks
Taxon	August 1980	August 1993
Acanthurus leucopareius	.02 61	< .07 27
Acanthurus nigrofuscus	.00 °	.06 29
Parupeneus porphyreus	.02 66	.05 30

^aMatched with *Scorpaena coniorta* on August 1993 survey. ^bAcanthurus olivaceus not observed on August 1993 survey. ^cAcanthurus nigrofuscus not observed on August 1980 survey.

Table 5.--August 1980 and August 1993 numerical densities (D) of reef fishes (N·10 m⁻²) at Midway Atoll,
Northwestern Hawaiian Islands. The top 30 fish taxa are ranked (Rank_B) in descending order of their grand means (D_{both}) for the two pooled ('BR' = Barrier, 'PR' = Patch) reef types, by sampling period. Analogous estimates are listed and ranked (Rank_A) for August 1993 samples, and also are provided for each reef type in each period.
Estimates are based on all available data for each period (1980: 9 stations--4 BR + 5 PR; 1993: 22 stations--10 BR + 12 PR. Also, see Tables 3, 4 captions.) Abbreviations for trophic levels and carnivore guilds are: Primary Consumers (Herbivores) [HERB]; Secondary Consumers (Corallivores [CO]; Benthic Carnivores [BC]; Zooplanktivores [PL]; and Piscivores [PISC]). An "abs" indicates absence from surveys. A dashed horizontal line separates the top 30 baseline taxa in August 1980 from lower-ranked taxa that ranked within the top 30 on the 1993 survey.

	Mean density (N·10 m ⁻²)								
		August 1980				August 1993			
Taxon	Rank	D _{BR}	D _{PR}	D _{both}	Rank	D_{BR}	D _{PR}	D_{both}	
Stegastes fasciolatus(HERB)	1	2.30	3.90	3.02	1	2.41	3.09	2.78	
Dascyllus albisella(PL)	2	.01	5.64	2.51	4	abs	2.10	1.05	
Thalassoma duperrey(BC)	3	2.33	2.59	2.44	2	2.33	2.04	2.17	
Chromis ovalis(PL)	4	.72	2.26	1.41	11	.21	.46	.34	
Stethojulis balteata(BC)	5	.70	.64	.68	8	.36	.46	.41	
Chromis hanui(PL)	6	.45	.71	.57	46	.02	.02	.02	
Chaetodon miliaris(PL)	7	.12	1.07	.55	12	<.01	.55	.30	
Apogon spp.(PL)	8	abs	.90	.45	3	<.01	2.81	1.53	
Acanthurus triostegus(HERB)	9	.80	<.01	.45	16	.23	.13	.18	

Table 5.--Continued.

		Me	ean de	nsity	(N·10	m ⁻²)		
	P	August	1980			August	1993	
Taxon	Rank _B	D _{BR}	D _{PR}	D_{both}	Rank	D _{BR}	D _{PR}	D _{both}
Cirripectes spp. (HERB)	10	.77	.03	.44	40	.05	abs	>.02
Thalassoma ballieui(BC)	11	.55	.26	.42	7	.40	.47	.43
Ctenochaetus strigosus(HERB)	12	.16	.73	.42	21	.11	.12	>.12
Labroides phthirophagus(BC)	13	.12	.64	.36	19	.04	.24	<.15
Scarid juveniles(HERB)	14	.33	.25	.29	5	.05	1.83	1.02
Kyphosus spp. (HERB)	15	.44	.07	.28	14	.42	.02	.20
Calotomus spp. (HERB)	16	abs	.55	.28	15	<.01	.35	.19
Aulostomus chinensis(PISC)	17	<.01	.39	.17	45	abs	.04	.02
Paracirrhites forsteri(BC)	18	.02	.35	.17	23	.01	.14	.08
Bodianus bilunulatus(BC)	19	.04	.33	.17	22	.08	.14	<.12
Abudefduf abdominalis(PL)	20	.24	.04	.15	10	.29	.47	<.39
Scarus perspi- cillatus(HERB)	21	.15	.14	.14	28	.11	.02	>.06
Chaetodon fremblii(BC)	22	.06	.25	.14	18	.02	.26	.15
Dendrochirus barberi(BC)	23	abs	.27	.14	42	abs	.05	.02
Cirrhitops fasciatus(BC)	24	.04	.22	.12	35	.02	.04	.03
Scorpaena spp. (BC) a	25	abs	.23	.12	64	abs	<.01	<.01

Table 5.--Continued.

		М	ean de	nsity	(N·10	m ⁻²)		
_	1	August	1980			Augu	st 199	3
Taxon	Rank	D _{BR}	D _{PR}	$D_{\mathtt{both}}$	Rank	D _{BR}	D _{PR}	D_{both}
Neoniphon sammara(PL)	26	<.01	.24	.11	43	<.01	.03	.02
Coris venusta(BC)	27	.07	.16	.11	9	.07	.66	.39
Acanthurus nigroris(HERB)	28	.21	abs	.10	20	.22	.05	>.12
Gomphosus varius(BC)	29	.16	.03	.10	51	.03	abs	<.02
Acanthurus olivaceus(HERB)	30	.20	abs	.10		abs	abs	.00
Parupeneus pleu- rostigma(BC)	59	.01	.04	<.03	6	<.01	.86	.47
Anampses cuvier(BC)	50	.03	.05	.04	13	.09	.37	.24
Cheilinus bimac- ulatus(BC)	88	abs	<.01	<.01	17	abs	.32	.16
Plectroglyphidodon johnstonianus(COR)	38	.04	.12	.08	24	.12	.05	<.08
Synodontid spp.(PISC)	35	.02	.18	.09	25	<.01	.13	.07
Canthigaster jactator(BC)	33	.03	.17	.09	26	<.02	.11	.07
Acanthurus leuco- pareius(HERB)	61	.05	abs	.02	27	.14	abs	<.07
Acanthurus nigro- fuscus(HERB)		abs	abs	.00	29	abs	.12	.06
Parupeneus por- phyreus(BC)	66	<.01	.04	.02	30	<.01	.09	.05
Top 30 fishes		11.0	22.9	16.4		7.8	18.5	13.4
Total fishes		12.7	25.8	18.5		8.4	19.2	14.3

^aScorpaena sp data on August 1980 survey matched with Scorpaena coniorta data on August 1993 survey

Table 6.--Listing and comparison of taxa "present in August 1980 but absent in August 1993" (P→A) and "absent in August 1980 but present in August 1993" (A→P) diver-observation surveys at Midway Atoll, Northwestern Hawaiian Islands. Listing is restricted to readily identifiable reef fishes that would have been recognized and recorded if encountered. See Appendix Table 2 for expanded listing and Table 5 caption for feeding guild abbreviations. Also summarized is the result of the binomial test, evaluating the relative number of P→As and A→Ps.

Taxon	P→A	A→P
Seriola dumerili(PISC)		×
Pseudocaranx dentex(BC)	x	
Aprion virescens(PISC)		x
Parupeneus bifasciatus(BC)		x
Parupeneus cyclostomus(BC)		x
Novaculichthys taeniourus(BC)		x
Cheilio inermis(BC)		x
Pterois sphex(BC)		x
Sebastapistes ballieui(BC)		x
Scorpaenopsis cacopsis(PISC)	x	
Scorpaenopsis diabolus(PISC)		x
Chaetodon multicinctus(CO)	×	
Exallias brevis(CO)	×	
Acanthurus olivaceus(HERB)	×	
Naso lituratus(HERB)	×	
Diodon holocanthus(BC)	×	
Diodon hystrix(BC)		x
Arothron hispidus(BC)	x	
Oplegnathus fasciatus(BC)	x	
Oplegnathus punctatus(BC)		x
Totals	9	11
	H _o : P→A	= A→P
	H, : P→A	

9 P→A to 11 A→P; binomial test, P>0.41

Table 7.--Summary of nominal "Before-After" changes in density (N·10 m⁻²) for the top 30 (baseline) taxa of reef fishes observed at Midway Atoll, Northwestern Hawaiian Islands. Taxa are classified by major trophic level and by feeding guild within the carnivore level. Densities of none of the 30 test taxa changed significantly once alpha levels were adjusted for the multiple comparisons. Also summarized are results of a binomial test of the relative number of nominal increases and decreases.

	Number of to	p 30 taxa
	Increasing	Decreasing
Herbivores	2	8
Secondary consumers	5	15
Benthic carnivores	3	9
Zooplanktivores	2	5
Corallivores	0	0
Piscivores	0	1
Total	7	23
	creases = # increases creases > # increases	

23/30 decreases; P = 0.003 (binomial test)

^aSignificance based on $\alpha_{2,crit} = 0.10/30 = .0033$

Table 8.--Summary of "Before-After" comparisons of densities (N·10 $\rm m^{-2}$) for major functional groupings of fishes at Midway Atoll, Northwestern Hawaiian Islands. Statistical conclusions are based on the results of parametric matched-pair (M-P) t-tests. Mean density data were matched by station and the grand mean of the signed differences (deltas) between sampling periods for all 8 (4 BR + 4 PR) test stations tested against the null and 2-tailed alternative hypotheses, H_0 : mean delta = 0 and H_a : mean delta \neq 0, respectively. Each estimated mean and one standard error of the mean (sem, in parentheses) are also provided for baseline (August 1980) samples.

		Baseline density $(N \cdot 10 \text{ m}^{-2})$			
Trophic level/guild	Mean (sem)	Pct of total	Apparent change — (pct) t	M-P P	t-test Conclusion
Total fishes	19.3 (4.0)	100	-32 2.1	1 .07	SIGª
Herbivores	6.0 (0.6)	31	-27 2.2	7 .06	$\mathtt{ns}^\mathtt{b}$
Secondary consumers	13.3 (3.7)	69	-32 1.7	0 .13	$\mathtt{ns}^\mathtt{b}$
Benthic carnivores	6.2 (1.0)	32	-21 2.5	3 .04	ns°
Planktivores	6.5 (2.6)	33	-60 1.6	3 .15	ns°
Corallivores	0.15 (.06)	< 1	+ 9 0.0	6 .95	ns°
Piscivores	0.52 (.32)	< 3	- 79 4. 7	8 .002	SIG°

 $^{^{}a}\alpha_{crit} = \alpha_{2,0.10}$

 $^{{}^{}b}\alpha_{crit} = \alpha_{2,0.10}/2 = .05$ ${}^{c}\alpha_{crit} = \alpha_{2,0.10}/4 = .025$

Table 9.—Summary of "Before-After" comparisons of relative (rank) densities for major functional groupings of fishes at Midway Atoll, Northwestern Hawaiian Islands. Statistical conclusions are based on results of nonparametric, Wilcoxon matched-pair signed-ranks (M-P S-R) tests. Density data were matched by station, and the signed differences (between sampling periods) ranked among the 8 test stations. The "T" statistic represents the sum of the smaller like-signed ranks (Siegel and Castellan, 1988).

Trophic	M-P S-R Test					
level/guild	T	P	Conclusion			
Total fishes	5	.10	SIGª			
Herbivores	4	.05 <p<.10< td=""><td>ns^b</td></p<.10<>	ns ^b			
Secondary consumers	8	>.10	ns ^b			
Benthic carnivores	6	>.10	ns°			
Planktivores	10	>.10	ns°			
Corallivores	14	>.10	ns°			
Piscivores	0	<<.05	SIG°			

 $^{^{}a}\alpha_{crit} = \alpha_{2,0.10}$

 $^{^{}b}\alpha_{crit} = \alpha_{2,0.10}/2 = .05$

 $^{^{}c}\alpha_{crit} = \alpha_{2,0.10}/4 = .025$

Table 10.--Summary results of parametric matched-pair (M-P) t-tests between "Before-After" densities (N·10 m⁻²) for major functional groupings of fishes at Midway Atoll, Northwestern Hawaiian Islands. Mean density data were matched by station and the signed differences (deltas) between sampling periods estimated separately for the barrier (n = 4) and patch reef (n = 4) test stations. See Table 8 caption for additional details.

		Baseline density (N·10 m ⁻²)		Apparent		M-P <i>t-</i> test		
Trophic level/guild	Reef Type	Mean	(sem)	change (pct)	t	P	Conclusion	
Total fishes	BR PR	12.4 22.9	(1.2) (1.3)	- 29 - 34	1.42	.25	ns ^a ns ^a	
Herbivores	BR PR	5.8 5.6	(1.2) (1.2)	- 37 - 15	1.78 2.01	.17	ns ^b ns ^b	
Secondary consumers	BR PR	6.4 17.1	(1.2) (1.4)	- 21 - 41	1.01 1.29	.39	ns ^b ns ^b	
Benthic carnivores	BR PR	4.7 6.8	(1.1) (1.4)	- 16 - 26	1.33 2.06	.28	ns° ns°	
Planktivores	BR PR	0.6 8.9	(3.0) (1.5)	- 68 - 52	1.08 1.13	.36	ns° ns°	
Corallivores	BR PR	0.08	(2.1) (2.3)	+133 - 72	-2.29 0.73	.11	ns° ns°	
Piscivores	BR PR	0.03 0.64	(1.6) (1.7)	- 94 - 85	2.78 3.79	.07	ns° ~SIG°	

 $^{^{}a}\alpha_{crit} = \alpha_{2,0.10}$

 $^{{}^{}b}\alpha_{crit} = {}^{a_{2,0.10}}/2 = .05$ ${}^{c}\alpha_{crit} = {}^{a_{2,0.10}}/4 = .025$

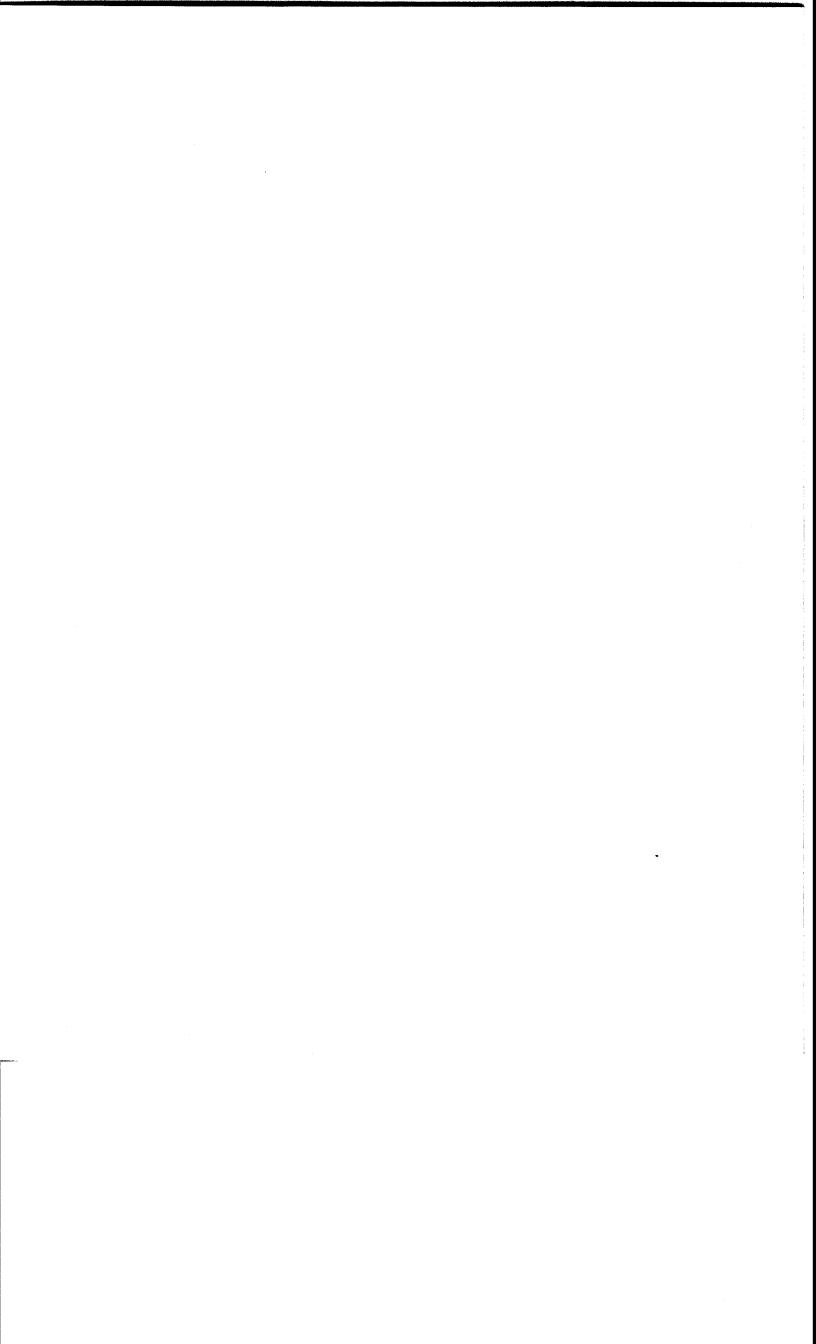
Table 11.—Summary results of tests to estimate the statistical power (1 minus Type II error), at $\alpha_2=0.05$ and at $\alpha_2=0.10$, using paired t-tests of "before minus after" deltas of mean density data for major functional groupings of fishes (all 8 test stations, both reef types) at Midway Atoll, Northwestern Hawaiian Islands. Also estimated are the sample sizes (number of stations sampled two times each in "before" and "after" periods) necessary to detect a two-fold change in density with a power of 0.80.

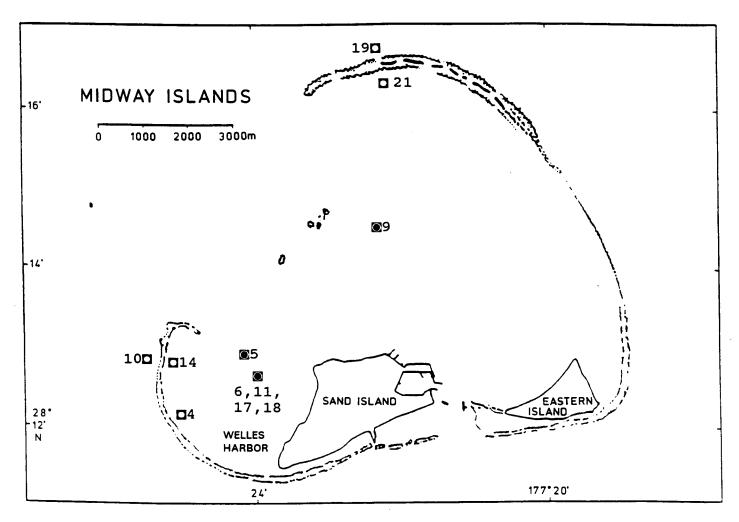
Variable	Observed change (pct)		to detect ange at α_2 =.10		ed ^b to ct 2x ge at α_2 =.10
Total fishes	-32	>.95	>.95	< 8	< 8
Herbivores	-27	>.95	>.95	< 8	< 8
Secondary consumers	-32	.81	.91	< 8	7
Benthic carnivores	-21	>.95	>.95	< 8	< 8
Zooplanktivores	-60	.21	.32	44	34
Corallivores	+ 9	.13	.22	88	68
Piscivores	-79	.51	. 65	16	12

^aFor log-transformed variables, a twofold change (log 2) equals a halving (50% decline) or a doubling (100% increase). ^bPower = .80



FIGURES





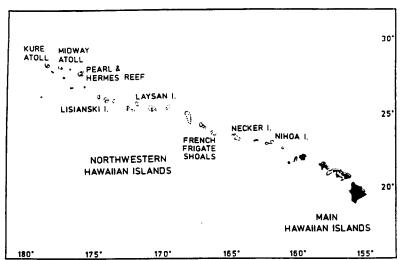


Figure 1.--Map of Midway Atoll, Northwestern Hawaiian Islands, showing the locations of the barrier reef (D) and lagoonal patch reef (E) stations at which reef fishes were surveyed in August 1980 and/or August 1993. Four pairs of patch reefs (test stations 6, 11, 17, and 18, each with its -A reference station) are indicated by a single symbol in southwest Welles Harbor; nontest/reference patch reef stations 5 & 5A and 9 & 9A are indicated by separate patch reef symbols west and north of Sand Island, respectively.

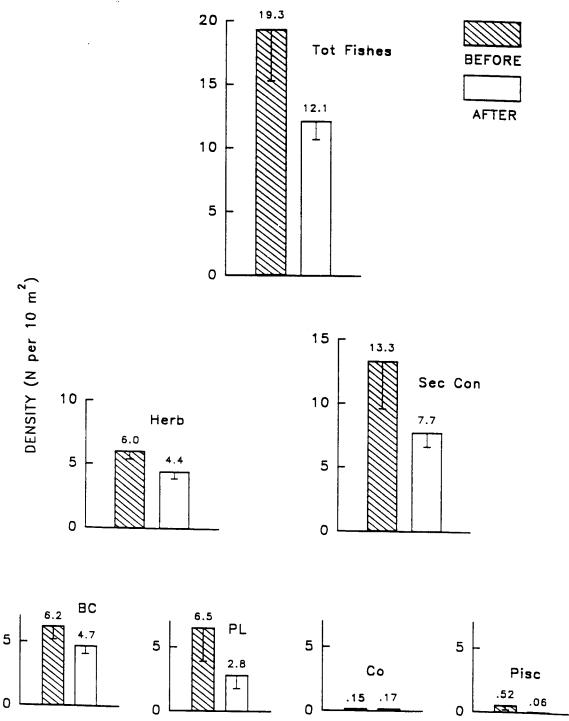


Figure 2.—Numerical densities (N·10 m⁻²) for total fishes (Tot Fish; top); two major trophic levels (Herbivores = Herb; Carnivores or Secondary Consumers = Sec Con; middle); and four carnivore guilds (Benthic Carnivores = BC; Zooplanktivores = PL; Corallivores = Co; and Piscivores = Pisc; bottom) at Midway Atoll during "Before" (August 1980) and "After" (August 1993) sampling periods. Estimates are unweighted grand means including the two (BR, PR) habitat types, based on the 8 (4 BR + 4 PR) test station means. One standard error (sem) of each estimate is provided.

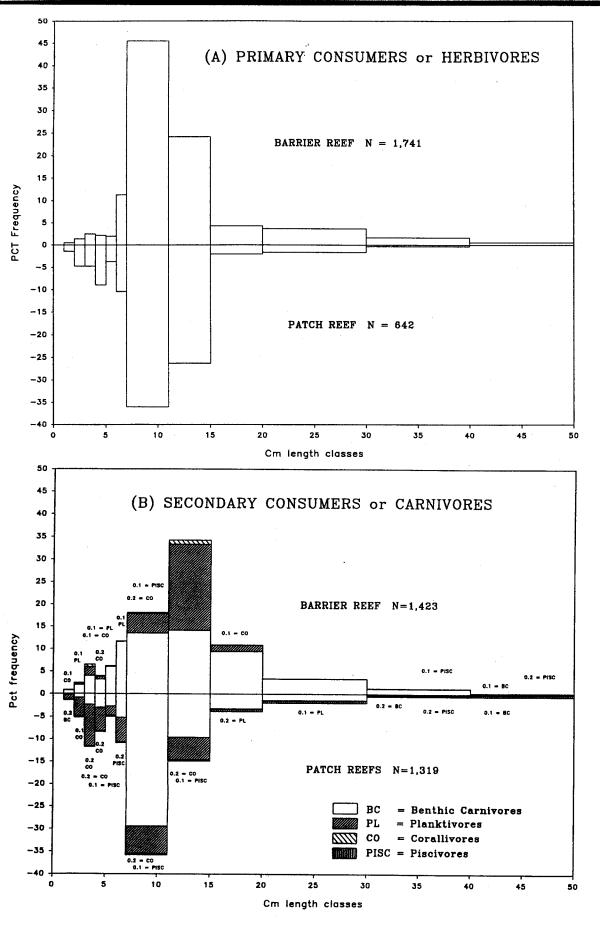


Figure 3.--Histograms of percentage frequency distributions of body length classes (cm SL) for (A) Primary Consumers or Herbivores and (B) Secondary Consumers or Carnivores. In each (A, B) panel, distributions are plotted for barrier reef stations and for patch reef stations above and below the horizontal axis, respectively. Within panel (B), Carnivore distributions are partitioned into Benthic Carnivore (BC), Zooplanktivore (PL), Corallivore (Co), and Piscivore (Pisc) guilds.

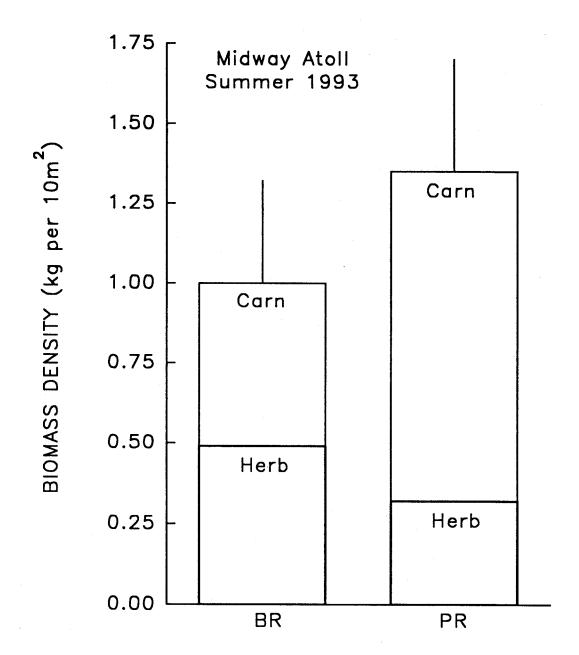
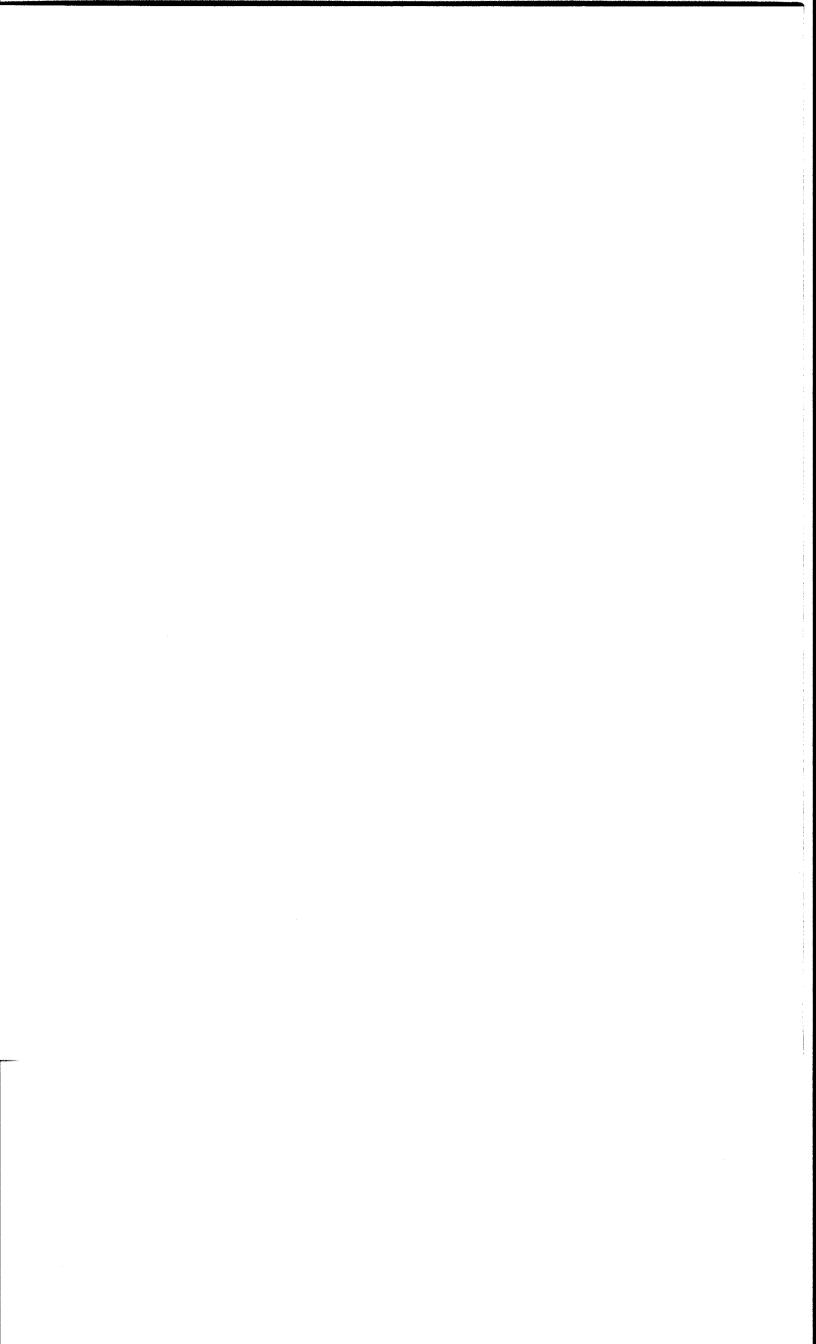


Figure 4.--Estimated mean biomass densities of herbivorous (Herb) and carnivorous (Carn) fishes on barrier (BR) and patch reefs (PR) at Midway Atoll during August 1993. Also indicated is one approximate standard error of the estimated biomass density for total (herbivorous plus carnivorous) fishes in each habitat.

APPENDIXES



Appendix Table 1.--Sampling dates and station specifics for baseline (August 1980) and August 1993 fish sampling at Midway Atoll, Northwestern Hawaiian Islands. Listing is ordered by station number within period. 'JDP' survey type is noted in order to reference the Midway sampling protocol to one of two used at FFS in July 1992 (DeMartini et al., 1993). Reef types are designated 'BR' for "Barrier Reef" and 'PR' for "Patch Reef", and sampling periods as 'PRE_' for "Before" (1980) and 'POST' for "After" (1993). "-A" suffixes to some After period stations indicate newly established reference stations; those lacking suffixes are either test or nontest stations (see Methods). "Nmbr taxa" refers to the number of species or subfamily-level taxa recognized on the transect. "Area" is the planar reef area used to standardize fish counts to density.

Date	Survey type	Reef type	Period	Station No.	Transect No.	Nmbr taxa	Area (m²)
06AUG80	JDP	PR	PRE_	6	1	30	286
06AUG80	JDP	PR	PRE_	6	2	32	286
08AUG80	JDP	PR	PRE_	6	3	33	286
09AUG80	JDP	BR	PRE_	10	1	35	500
09AUG80	JDP	PR	PRE_	11	1	37	154
09AUG80	JDP	PR	PRE_	11	2	43	154
11AUG80	JDP	BR	PRE_	14	1	39	500
13AUG80	JDP	BR	PRE_	14	2	35	500
19AUG80	JDP	PR	PRE_	16	1	40	500
19AUG80	JDP	PR	PRE_	16	2	38	500
19AUG80	JDP	PR	PRE	17	1	34	97
19AUG80	JDP	PR	PRE_	17	2	31	97
20AUG80	JDP	PR	PRE	18	1	32	54
20AUG80	JDP	PR	PRE_	18	2	31	54
24AUG80	JDP	BR	PRE_	19	1	44	500
24AUG80	JDP	BR	PRE_	19	2	44	500
24AUG80	JDP	BR	PRE_	21	1	24	500
25AUG80	JDP	BR	PRE_	21	2	26	500
09AUG93	JDP	BR	POST	4	1	26	500
09AUG93	JDP	BR	POST	4	2	17	500
09AUG93	JDP	BR	POST	4A	1	25	500
09AUG93	JDP	BR	POST	4A	2	18	500
11AUG93	JDP	PR	POST	5	1	18	109
11AUG93	JDP	PR	POST	5	2	17	109
11AUG93	JDP	PR	POST	5 A	1	25	168
11AUG93	JDP	PR	POST	5A		25	168
10AUG93	JDP	PR	POST	6	2 1	21	154

Appendix Table 1.--Continued.

Date	Survey type	Reef type	Period	Station No.	Transect No.	Nmbr taxa	Area (m²)
10AUG93	JDP	PR	POST	6	2	21	154
13AUG93	JDP	PR	POST	6A	1	16	191
13AUG93	JDP	PR	POST	6A	2	20	191
12AUG93	JDP	PR	POST	9	1	13	140
12AUG93	JDP	PR	POST	9	2	13	140
12AUG93	JDP	PR	POST	9A	1	20	140
12AUG93	JDP	PR	POST	9 A	2	20	140
08AUG93	JDP	BR	POST	10	1	38	500
08AUG93	JDP	BR	POST	10	2	32	500
11AUG93	JDP	BR	POST	10A	1	36	500
11AUG93	JDP	BR	POST	10A	2	27	500
10AUG93	JDP	PR	POST	11	1	17	87
10AUG93	JDP	PR	POST	11	2	14	87
13AUG93	JDP	PR	POST	11A	1	21	26
13AUG93	JDP	PR	POST	11A	2	22	26
08AUG93	JDP	BR	POST	14	1	21	500
08AUG93	JDP	BR	POST	14	2	22	500
08AUG93	JDP	BR	POST	14A	1	27	500
08AUG93	JDP	BR	POST	14A	2	27	500
09AUG93	JDP	PR	POST	17	1	28	168
09AUG93	JDP	PR	POST	17	2	29	168
13AUG93	JDP	PR	POST	17A	1	18	87
13AUG93	JDP	PR	POST	17A	2	20	87
10AUG93	JDP	PR	POST	18	1	10	35
10AUG93	JDP	PR	POST	18	2	16	35
10AUG93	JDP	PR	POST	18A	1	13	62
10AUG93	JDP	PR	POST	18A	2	13	62
07AUG93	JDP	BR	POST	19	1	35	500
07AUG93	JDP	BR	POST	19	2	33	500
07AUG93	JDP	BR	POST	19A	1	28	500
07AUG93	JDP	BR	POST	19A	2	31	500
07AUG93	JDP	BR	POST	21	ī	26	500
07AUG93	JDP	BR	POST	21	2	20	500
12AUG93	JDP	BR	POST	21A	ĩ	22	500
12AUG93	JDP	BR	POST	21A	2	21	500

Appendix Table 2.--List of all fishes (species and higher taxa within family) encountered on transects and free-swims (length estimation task, August 1993 only) at Midway Atoll during the August 1980 baseline ('PRE_') survey and the August 1993 ('POST') survey. 'x' = presence; 'n/r' = "not recorded". "IDNO" designates 4-digit taxonomic computer code. The multiple records for each taxon recorded in the 'POST' period refer to Divers 1, 2 and 3.

		PE	RIOD			
FAMILY/taxon	IDNO	'PRE_'	• 1	POSI	. 1	
CARCHARHINIDAE	100	x		х		
Carcharhinus amblyrhynchos	102	x		x		
CARANGIDAE	200	x	x		x	
Caranx ignobilis	201	x	x	x	X	
Caranx melampygus	202	x		X	x	
Seriola dumerili	205	n/r	x			
Pseudocaranx dentex	206	х	not	rec	orded	
MURAENIDAE	300	x	x	x	x	
Gymnothorax flavimarginatus	301	x				
Gymnothorax spp.	302	x	x	x	x	
Gymnothorax eurostus	304	x				
Gymnothorax steindachneri	308	x				
Enchelynassa sp	309	x				
Enchelycore pardalis	310	x				
AULOSTOMIDAE	400	x	x	x	x	
Aulostomus chinensis	401	x	x	x	x	
FISTULARIDAE	500	x	x	x	x	
Fistularia commersonii	501	x	x	X	X	
LUTJANIDAE	600	n/r			X	
Aprion virescens	602	n/r			x	
SYNODONTIDAE	700	×	х	x	x	
Synodus spp.	701	x	x	X	x	
HOLOCENTRIDAE	800	x	x	x	X	
Sargocentron sp	801	x	x	X	x	
Neoniphon sammara	802	x	x		X	
Myripristis spp.	803	X	x	x	x	
Sargocentron xantherythrum	808	X				
APOGONIDAE	900	X	x	x	x	
Apogon spp.	901	X	·x	x	x	
Foa brachygramma	906		x			
MULLIDAE	1100	x	x	x	x	
Mulloidichthys flavo-						
lineatus	1102	x			x	
Mulloidichthys vanicolensis		×	x	х	x	
Parupeneus bifasciatus	1104	n/r	x	x	x	
Parupeneus cyclostomus	1106	n/r	X	A	42	
Parupeneus multifasciatus	1107	X		x	x	
		42		^	•	

Appendix Table 2.--Continued.

]	PERIOD
FAMILY/taxon	IDNO	'PRE_'	'POST'
Parupeneus pleurostigma	1108	x	x x x
Parupeneus porphyreus	1109	x	x x x
Parupeneus sp	1110		хх
LABRIDAE	1200	x	ххх
Anampses chrysocephalus	1201	x	x x
Anampses cuvier	1202	x	x x x
Bodianus bilunulatus	1203	x	ххх
Cheilinus unifasciatus	1204	X	ххх
Coris flavovittata	1205	x	ххх
Coris venusta	1208	x	$\mathbf{x} \mathbf{x} \mathbf{x}$
Epibulus insidiator	1209	x	x
Gomphosus varius	1210	x	x x x
Labrid sp	1212		x
Labroides phthirophagus	1213	X	x x x
<i>Macropharyngodon</i> sp	1215	x	x x x
Novaculichthys taeniourus	1216	n/r	хх
Pseudocheilinus sp	1217	x	$\mathbf{x} \mathbf{x} \mathbf{x}$
Stethojulis balteata	1218	X	x x x
Thalassoma ballieui	1219	x	x x x
Thalassoma duperrey	1220	X	x x x
Halichoeres ornatissimus	1221	x	x x
Pseudocheilinus octotaenia	1222	X	x x
Macropharyngodon geoffroy	1223	x	
Cheilinus bimaculatus	1227	X	x x x
Thalassoma fuscum	1229	{= T.purp.}	x x x
Thalassoma purpureum	1231	X	{cf T.fuscum}
Cymolutes sp	1232	X	
Cymolutes leclusei	1233		x x
Cheilio inermis	1234	n/r	x x x
CIRRHITIDAE	1300	x	$\mathbf{x} \mathbf{x} \mathbf{x}$
Cirrhitops fasciatus	1301	x	x x x
Paracirrhites arcatus	1303	X	x x
Paracirrhites forsteri	1304	x	x x x
Cirrhitus pinnulatus	1305	x	x x
SCORPAENIDAE	1400	x	x x x
Dendrochirus barberi	1401	×	x x x
Pterois sphex	1402	n/r	x x x
Pterois sp	1403		x
Sebastapistes ballieui	1405	n/r	x
Sebastapistes coniorta	1406	X	х х
Scorpaenopsis cacopsis	1407	x	- not recorded
Scorpaena sp	1408	X	
Scorpaenopsis diabolus	1409	n/r	X
PRIACANTHIDAE	1500	X	x x x
(Hetero) priacanthus spp. CHEILODACTYLIDAE	1501	X	X X X
	1600	X	x x x
Cheilodactylus vittatus	1601	X	x x x

Appendix Table 2.--Continued.

			PERIOD
FAMILY/taxon	IDNO	'PRE_'	'POST'
BALISTIDAE	1700	x	x x x
Melichthys niger	1701	x	x x x
CANTHIGASTERIDAE	1800	x	x x x
Canthigaster jactator	1801	x	x x x
OSTRACIIDAE	1900	x	x x
Ostracion meleagris	1901	x	хх
MONACANTHIDAE	2000	x	x x x
Pervagor spilosoma	2002	x	x x x
POMACANTHIDAE	2100	x	x x x
Centropyge potteri	2101	x	x x x
CHAETODONTIDAE	2200	x	x x x
Chaetodon auriga	2201	x	x x x
Chaetodon fremblii	2202	x	x x x
Chaetodon miliaris	2203	x	x x x
Chaetodon multicinctus	2204	x	not recorded
Chaetodon ornatissimus	2205	x	x x x
Chaetodon trifasciatus	2209	x	x x x
Chaetodon unimaculatus	2210	x	x
Forcipiger flavissimus	2211	x	x x
BLENNIIDAE	2300	x	x x
Cirripectes spp.	2302	x	x x
Exallias brevis	2304	x	not recorded
Istiblennius gibbifrons	2308	x	
POMACENTRIDAE	2400	x	x x x
Abudefduf abdominalis	2401	x	x x x
Chromis hanui	2402	x	x x x
Chromis ovalis	2403	×	x x x
Chromis vanderbilti	2404	x	x x
Dascyllus albisella	2406	x	x x x
Plectroglyphidodon			
johnstonianus	2408	x	x x x
Stegastes fasciolatus	2410	×	x x x
KYPHOSIDAE	2500	×	x x x
Kyphosus spp.	2501	×	x x x
SCARIDAE	2600	x	x x x
Scarus dubius	2601	×	x
Scarus perspicillatus	2602	×	xxx
Scarus sordidus	2603	x	X X
Scarid spp. juvenile	2605	X	X X X
Calotomus sp	2607	X	XXX
ACANTHURIDAE	2700	x	XXX
Acanthurus nigrofuscus	2705	X	X
Acanthurus nigroris	2706	X	
Acanthurus olivaceus	2707	X	x x x not recorded
Acanthurus triostegus	2708	X	
Ctenochaetus strigosus	2710 2710	X	
Naso lituratus	2711	X X	X X X
	2,11	A	not recorded

Appendix Table 2.--Continued.

FAMILY/taxon	IDNO	PERIOD	
		'PRE_'	'POST'
Naso unicornis	2712	x	x x x
Zebrasoma flavescens	2713	x	x x x
Acanthurus leucopareius	2717	x	x x x
Zebrasoma veliferum	2722	x	ххх
Naso sp	2723	x	
ZANCLIDAE	2800	x	$\mathbf{x} \cdot \mathbf{x} \cdot \mathbf{x}$
Zanclus cornutus	2801	x	$\mathbf{x} \cdot \mathbf{x} \cdot \mathbf{x}$
DIODONTIDAE	2900	x	x
Diodon holocanthus	2901	x	not recorded
Diodon histrix	2902	n/r	x
TETRAODONTIDAE	3100	x	not recorded
Arothron hispidus	3102	x	not recorded
SERRANIDAE	3200	x	x x
Epinephelus quernus	3202	x	x x
GOBIIDAE	3400	x	$\mathbf{x} \mathbf{x} \mathbf{x}$
Gnatholepis anjerensis	3402	x	$\mathbf{x} \mathbf{x} \mathbf{x}$
OPHICHTHIDAE	3600	x	
OPHIDIIDAE	3700	x	
Brotula multibarbata	3702	x	
OPLEGNATHIDAE	3900	x	x x x
Oplegnathus fasciatus	3901	x	not recorded
Oplegnathus punctatus	3902	n/r	X

